

New subgeneric names for the most commercially important shrimp genus *Penaeus* Fabricius, 1798 (Crustacea, Decapoda, Penaeidae)

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Abstract

Although a recent comprehensive molecular phylogenetic study on *Penaeus* Fabricius, 1798 reinstated a single genus for these economically important shrimps, several clades in the molecular phylogenetic tree do not have formal names. Subgeneric names are given herein to five of these clades if *Penaeus* is to be split. A key to the subgenera in *Penaeus* is also provided.

Keywords

Key, marine invertebrates, new subgenus, nomenclature, stability, taxonomy

Introduction

The most comprehensive study to date on the phylogenetic relationships amongst the members of the genus *Penaeus* s.l. Fabricius, 1798 was by Yang et al. (2023), which suggested that a single genus should be reinstated for these commercially important shrimps. Their study also proposes that if those molecular clades revealed in the phylogenetic tree of *Penaeus* s.l. (Yang et al. 2023: fig. 3) are recognized as taxonomic groups, the use of subgenera is preferable; the use of this rank would also reduce confusion and maintain stability for non-taxonomists who use the name.

In their phylogenetic study, Yang et al. (2023: fig. 3) showed that up to 11 subgeneric-level clades can be recognized. While many of these clades have been named in the past, five of them, however, remain un-named. In the interest of nomenclatural stability and consistency in discussing their systematics, I here propose to apply formal names for them. This action is justified especially if the peculiar taxon *Marsupenaeus* Tirmizi, 1971, which has a very specialized pouch-like thelycum, is to be maintained.

A key to these 11 subgenera is also provided even though all important characters used have already been proved to be neither synapomorphic nor evolutionary informative in Yang et al. (2023).

Systematic account

Penaeus (Penaeus) Fabricius, 1798

Type species. *Penaeus monodon* Fabricius, 1798.

Gender of subgenus. Masculine.

Diagnosis. Rostrum generally armed with 3 ventral teeth. Median sulcus on posterostral carina shallow to indistinct. Adrostral sulcus extending posteriorly more or less to level of epigastric tooth. Gastrofrontal carina absent. Cervical carina with dorsal end a distance from dorsal carapace. Hepatic carina distinct, nearly horizontal. First pereiopod with distinct ischial spine. Fifth pereiopod without exopod. Sixth abdominal somite completely lacking dorsolateral sulcus. Telson without lateral spines. Thelycum closed.

Species included. *Penaeus (Penaeus) monodon* Fabricius, 1798, *Penaeus (Penaeus) simplex* Chan, Muchlisin & Hurzaid, 2021.

Remarks. Although this is the nominotypical subgenus of *Penaeus*, it is unusual in lacking an epipod on the fifth pereiopod; the subgenus contains only two of the 32 recognized species in the genus.

Penaeus (Melicertus) Rafinesque, 1814

Type species. *Melicertus tigrinus* Rafinesque, 1814 (= *Cancer kerathurus* Forskål, 1775).

Gender of subgenus. Masculine.

Diagnosis. Rostrum usually bearing 1 ventral tooth. Median sulcus at posterostral carina deep, long, about half carapace length. Adrostral sulcus as wide as posterostral carina, extending to near posterior margin of carapace. Gastrofrontal carina distinct and with posterior end turning anterodorsally. Cervical carina long, extending almost to dorsal carapace. Hepatic carina distinct. First pereiopod with ischial spine small to absent. Fifth pereiopod bearing exopod. Sixth abdominal somite completely lacking dorsolateral sulcus. Telson with 3 pairs of lateral spines. Thelycum closed.

Species included. *Penaeus (Melicertus) kerathurus* (Forskål, 1775).

Remarks. Amongst the members of *Penaeus*, only this subgenus has a geographical distribution in the eastern Atlantic and the Mediterranean. This subgenus is also unique in the genus by having a long cervical carina which has the dorsal end almost reaching the dorsal carapace.

Penaeus (Fenneropenaeus) Pérez Farfante, 1969

Type species. *Penaeus indicus* H. Milne Edwards, 1837.

Gender of subgenus. Masculine.

Diagnosis. Rostrum generally bearing 2–5 ventral teeth. Postrostral carina without median sulcus, sometimes with pits or sunken areas. Adrostral sulcus extending posteriorly more or less to epigastric tooth. Gastrofrontal carina absent. Cervical carina with dorsal end a distance from dorsal carapace. Hepatic carina often absent, if present, ill-defined. First pereiopod with small to minute ischial spine. Fifth pereiopod bearing exopod. Sixth abdominal somite completely lacking dorsolateral sulcus. Telson without lateral spines. Thelycum closed.

Species included. *Penaeus (Fenneropenaeus) chinensis* (Osbeck, 1765), *Penaeus (Fenneropenaeus) indicus* H. Milne Edwards, 1837, *Penaeus (Fenneropenaeus) merguiensis* De Man, 1888, *Penaeus (Fenneropenaeus) penicillatus* Alcock, 1905, *Penaeus (Fenneropenaeus) silasi* Muthu & Motoh, 1979.

Remarks. This subgenus is unique in the genus by lacking a distinct hepatic carina. Only *P. (Fenneropenaeus) chinensis* bears an ill-defined hepatic carina while all other species of *Penaeus (Fenneropenaeus)* lack a hepatic carina. As mentioned in Ma et al. (2011) and Yang et al. (2023), *Fenneropenaeus konkani* Chanda & Bhattacharya, 2003 is very likely to be an invalid taxon with a deformed rostrum and a synonym of a known species of *Penaeus (Fenneropenaeus)*.

Penaeus (Litopenaeus) Pérez Farfante, 1969

Type species. *Penaeus vannamei* Boone, 1931.

Gender of subgenus. Masculine.

Diagnosis. Rostrum usually bearing 2–4 ventral teeth. Postrostral carina without median sulcus, only sometimes with pits or sunken areas. Adrostral sulcus extending posteriorly more or less to epigastric tooth. Gastrofrontal carina absent. Cervical carina with dorsal end a distance from dorsal carapace. Hepatic carina distinct. First pereiopod with distinct ischial spine. Fifth pereiopod bearing exopod. Sixth abdominal somite bearing weak to distinct dorsolateral sulcus. Telson without lateral spines. Thelycum open.

Species included. *Penaeus (Litopenaeus) occidentalis* Streets, 1871; *Penaeus (Litopenaeus) schmitti* Burkenroad, 1936; *Penaeus (Litopenaeus) setiferus* (Linnaeus, 1767); *Penaeus (Litopenaeus) stylirostris* Stimpson, 1871; *Penaeus (Litopenaeus) vannamei* Boone, 1931.

Remarks. This subgenus is unique in the genus by having an open thelycum.

***Penaeus (Marsupenaeus)* Tirmizi, 1971**

Type species. *Penaeus canaliculatus* var. *japonicus* Bate, 1888.

Gender of subgenus. Masculine.

Diagnosis. Rostrum generally armed with 1 ventral tooth. Median sulcus at postrostral carina deep, long, about half carapace length. Adrostral sulcus extending to near posterior margin of carapace, posterior part somewhat narrower than postrostral carina. Gastrofrontal carina distinct, with posterior end turning anterodorsally. Cervical carina with dorsal end a distance from dorsal carapace. Hepatic carina distinct. First pereiopod with ischial spine minute or absent. Fifth pereiopod bearing exopod. Sixth abdominal somite completely lacking dorsolateral sulcus. Telson with 3 pairs of lateral spines. Thelycum pouch-like.

Species included. *Penaeus (Marsupenaeus) japonicus* Bate, 1888, *Penaeus (Marsupenaeus) pulchricaudatus* Stebbing, 1914.

Remarks. Although this subgenus is unique in the genus by having a highly specialized pouch-like thelycum, males and juveniles are morphologically very similar to those of the subgenus *Penaeus (Oleopenaeus)* subgen. nov., except for coloration [see “Remarks” under *Penaeus (Oleopenaeus)* subgen. nov.].

***Penaeus (Farfantepenaeus)* Burukovsky, 1972**

Type species. *Penaeus brasiliensis* var. *aztecus* Ives, 1891.

Gender of subgenus. Masculine.

Diagnosis. Rostrum usually bearing 2 ventral teeth. Median sulcus at postrostral carina generally distinct, long. Adrostral sulcus extending to near posterior margin of carapace. Gastrofrontal carina distinct, with posterior end not turning anteriorly. Cervical carina with dorsal end a distance from dorsal carapace. Hepatic carina distinct. First pereiopod with strong ischial spine. Fifth pereiopod bearing exopod. Sixth abdominal somite with distinct dorsolateral sulcus. Telson without lateral spines. Thelycum closed.

Species included. *Penaeus (Farfantepenaeus) aztecus* Ives, 1891, *Penaeus (Farfantepenaeus) brasiliensis* Latreille, 1817, *Penaeus (Farfantepenaeus) brevirostris* Kingsley, 1878, *Penaeus (Farfantepenaeus) californiensis* Holmes, 1900, *Penaeus (Farfantepenaeus) duorarum* Burkenroad, 1939, *Penaeus (Farfantepenaeus) isabelae* Tavares & Gusmão, 2016, *Penaeus (Farfantepenaeus) notialis* Pérez Farfante, 1967, *Penaeus (Farfantepenaeus) paulensis* Pérez Farfante, 1967, *Penaeus (Farfantepenaeus) subtilis* Pérez Farfante, 1967.

Remarks. This subgenus together with *Penaeus (Litopenaeus)* are often called the American *Penaeus*. Morphologically these two subgenera are markedly different from each other and had long been thought to be evolutionary far apart (see Burkenroad 1934; Kubo 1949; Pérez Farfante 1969; Dall et al. 1990; von Sternberg and Motoh 1995; Pérez Farfante and Kensley 1997; von Sternberg 1997). They are, however, very closely related genetically (see Yang et al. 2023). At present only one morphological character, the sixth abdominal somite with dorsolateral sulcus, is found to separate the

American *Penaeus* from other congeneric species. Recent molecular analysis has suggested that *P. (Farfantepenaeus) notialis*, originally described as a subspecies of *P. (Farfantepenaeus) duorarum*, may not be distinct at the species level (Timm et al. 2019).

Penaeus (Altiopeneaus) subgen. nov.

<https://zoobank.org/594460D1-98BB-4C4B-9902-068EB4E1DEBA>

Type species. *Penaeus marginatus* Randall, 1840.

Gender of subgenus. Masculine.

Diagnosis. Rostrum usually armed with 2 ventral teeth. Postrostral carina lacking median sulcus. Adrostral sulcus as wide as postrostral carina, extending to near posterior margin of carapace. Gastrofrontal carina distinct, with posterior end turning antero-dorsally. Cervical carina with dorsal end a distance from dorsal carapace. Hepatic carina distinct. First pereiopod with strong ischial spine. Fifth pereiopod bearing exopod. Sixth abdominal somite completely lacking dorsolateral sulcus. Telson with 3 pairs of lateral spines. Thelycum closed.

Etymology. The name *Altiopeneaus* (from the Latin *altio* for deeper) alluding to members of this subgenus which have a deeper vertical (depth) distribution than other *Penaeus*.

Species included. *Penaeus (Altiopeneaus) marginatus* Randall, 1840

Remarks. This taxon corresponds to “gen. nov. 5” in the 11-genus scheme of fig. 3 in Yang et al. (2023). This subgenus is unusual in the genus in inhabiting deeper waters (see Chan 1998). It is also unique amongst the “grooved” species by completely lacking a median sulcus on the postrostral carina.

Penaeus (Eopenaeus) subgen. nov.

<https://zoobank.org/4BBD630C-8CB8-4AEE-89F0-949C019DFFAB>

Type species. *Penaeus semisulcatus* De Haan, 1844.

Gender of subgenus. Masculine.

Diagnosis. Rostrum generally bearing 3 or 4 ventral teeth. Median sulcus on postrostral carina present or absent. Adrostral sulcus extending posteriorly more or less to level of epigastric tooth. Gastrofrontal carina absent. Cervical carina with dorsal end a distance from dorsal carapace. Hepatic carina distinct and usually sloping anteroventrally. First pereiopod with distinct ischial spine. Fifth pereiopod bearing exopod. Sixth abdominal somite completely lacking dorsolateral sulcus. Telson without lateral spines. Thelycum closed.

Etymology. The name *Eopenaeus* (from the Greek *Eos* for others) refers to this subgenus being morphologically close to the nominotypical subgenus of *Penaeus* while the molecular data revealed that this subgenus is actually more derived than *Penaeus* (*Penaeus*) (Yang et al. 2023).

Species included. *Penaeus (Eopenaeus) esculentus* Haswell, 1879, *Penaeus (Eopenaeus) semisulcatus* De Haan, 1844.

Remarks. This taxon corresponds to “gen. nov. 1” in the 11-genus scheme of fig. 3 in Yang et al. (2023). Morphologically this subgenus is similar to *Penaeus* (*Litopenaeus*). Other than having different types of thelycum, these two subgenera can be distinguished by the body coloration [banded in *Penaeus* (*Eopenaeus*) subgen. nov. but not banded in *Penaeus* (*Litopenaeus*)] and the development of the dorsolateral sulcus on the sixth abdominal somite [weak to distinct in *Penaeus* (*Litopenaeus*) but completely absent in *Penaeus* (*Eopenaeus*) subgen. nov.]. Pérez Farfante (1969) and Pérez Farfante and Kensley (1997) also pointed out that there are differences in the shape of the petasma between these two subgenera, with the ventral costa reaching or not reaching the distal margin of the lateral lobe in *Penaeus* (*Eopenaeus*) subgen. nov. and *Penaeus* (*Litopenaeus*), respectively.

Penaeus (Ischiopenaeus) subgen. nov.

<https://zoobank.org/716AD2C7-AEDE-4549-94B3-65378708E2DB>

Type species. *Penaeus longistylus* Kubo, 1943.

Gender of subgenus. Masculine.

Diagnosis. Rostrum generally armed with 1 ventral tooth. Median sulcus at postrostral carina deep but distinctly shorter than half carapace length. Adrostral sulcus somewhat wider than postrostral carina and extending to near posterior margin of carapace. Gastrofrontal carina distinct and with posterior end turning anterodorsally. Cervical carina with dorsal end a distance from dorsal carapace. Hepatic carina distinct. First pereiopod with strong ischial spine. Fifth pereiopod bearing exopod. Sixth abdominal somite completely lacking dorsolateral sulcus. Telson with 3 pairs of lateral spines. Thelycum closed.

Etymology. The name *Ischiopenaeus* alludes to the presence of a strong ischial spine at the first pereiopod in this subgenus of *Penaeus*.

Species included. *Penaeus (Ischiopenaeus) longistylus* Kubo, 1943

Remarks. This taxon corresponds to “gen. nov. 4” in the 11-genus scheme of fig. 3 in Yang et al. (2023). This subgenus differs from almost all the non-American “grooved” species in the first pereiopod bearing a strong ischial spine (vs. small to absent). Another non-American “grooved” species with a strong ischial spine at the first pereiopod is *P. (Altiopenaeus) marginatus*, which lacks a median sulcus on the postrostral carina and generally has two ventral rostral teeth. Thus, the enigmatic *Melicertus similis* Chanda & Bhattacharya, 2002 described from the Andaman Sea likely represents juveniles of *P. (Ischiopenaeus) longistylus* as its original description and figures (Chanda and Bhattacharya 2002: figs 1, 6) indicated the presence of postrostral sulcus, only one ventral rostral tooth and the first pereiopod bearing a strong ischial spine. The “absence” of lateral spines on the telson in *Melicertus similis* is likely evidence that Chanda and Bhattacharya’s (2002) material are juveniles (total length including rostrum less than 80 mm) as juveniles of *Penaeus* generally have the lateral spines on the telson rather small and can be easily detached or overlooked.

Penaeus (Oleopenaeus) subgen. nov.

<https://zoobank.org/12C57BB8-B27D-4AD7-B3C3-2AD35708E4EC>

Type species. *Penaeus latisulcatus* Kishinouye, 1896.

Gender of subgenus. Masculine.

Diagnosis. Rostrum generally armed with 1 ventral tooth. Median sulcus at postrostral carina deep, long, about half carapace length. Adrostral sulcus as wide as postrostral carina, extending to near posterior margin of carapace. Gastrofrontal carina distinct, with posterior end turning anterodorsally. Cervical carina with dorsal end a distance from dorsal carapace. Hepatic carina distinct. First pereiopod with ischial spine minute or absent. Fifth pereiopod bearing exopod. Sixth abdominal somite completely lacking dorsolateral sulcus. Telson with 3 pairs of lateral spines. Thelycum closed.

Etymology. The name *Oleopenaeus* (from the Latin *olea* for olive coloured) refers to the more or less uniform greenish-yellow body coloration of this group of *Penaeus* shrimps.

Species included. *Penaeus (Oleopenaeus) hathor* Burkenroad, 1959, *Penaeus (Oleopenaeus) latisulcatus* Kishinouye, 1896, *Penaeus (Oleopenaeus) plebejus* Hess, 1865.

Remarks. This taxon corresponds to “gen. nov. 3” in the 11-genus scheme of fig. 3 in Yang et al. (2023). Except for the shape of the thelycum and body coloration, this subgenus is morphologically very similar to *Penaeus (Marsupenaeus)* (see Chan 1998; Tsoi et al. 2014). The thelycum is of the normal closed type in *Penaeus (Oleopenaeus)* subgen. nov. but pouch-like in *Penaeus (Marsupenaeus)*. With regards to the colour in life, the body is not banded in *Penaeus (Oleopenaeus)* subgen. nov. but is covered with thick cross bands in *Penaeus (Marsupenaeus)*. The taxonomic status of *P. (O.) hathor* is still uncertain if it merely represents a subspecies of *P. (O.) latisulcatus* or even a synonym of the latter, as both morphological and genetic differences between these two taxa are rather minor (Holthuis 1980; Miquel 1984; Chan 1998; Ma et al. 2011; 0.8% sequence divergence in COIb 512 bp, Yang et al. 2023: table 1).

Penaeus (Plagosopenaeus) subgen. nov.

<https://zoobank.org/B5F2E1F8-8B97-402E-AC9A-57B8AFCC43EB>

Type species. *Palæmon canaliculatus* Olivier, 1811.

Gender of subgenus. Masculine.

Diagnosis. Rostrum generally bearing 1 ventral tooth. Median sulcus at postrostral carina deep, long, about half carapace length. Adrostral sulcus as wide as postrostral carina, extending to near posterior margin of carapace. Gastrofrontal carina distinct, posterior end turning anterodorsally. Cervical carina with dorsal end a distance from dorsal carapace. Hepatic carina distinct. First pereiopod with ischial spine minute or absent. Fifth pereiopod bearing exopod. Sixth abdominal somite completely lacking dorsolateral sulcus. Telson without lateral spines. Thelycum closed.

Etymology. The name *Plagosopenaeus* (from the Latin *plagosus* for banded) refers to this subgenus of *Penaeus*, which has a very striking banded body coloration.

Species included. *Penaeus (Plagosopenaeus) canaliculatus* (Olivier, 1811).

Remarks. This taxon corresponds to “gen. nov. 2” in the 11-genus scheme of fig. 3 in Yang et al. (2023). Morphologically, including coloration, this subgenus is extremely similar to *Penaeus (Marsupenaeus)* (see Yu and Chan 1986; Chan 1998) and such close affinity is also supported by the molecular data (Yang et al. 2023: figs 2, 3). *Penaeus (Plagosopenaeus)* subgen. nov. only differs from *Penaeus (Marsupenaeus)* in lacking lateral spines on the telson (vs. bearing three pairs of lateral spines), the thelycum not pouch-like and the last transverse band on the sixth abdominal somite not interrupted (Chan 1998).

Key to subgenera in *Penaeus*

- 1 Adrostral sulcus and carina long, reaching near posterior margin of carapace; gastrofrontal carina present 2
- Adrostral sulcus and carina short, extending posteriorly at most to mid-carapace around level of epigastric tooth; gastrofrontal carina absent 8
- 2 Gastrofrontal carina not turning anteriorly at posterior end; sixth abdominal tergite with well-defined dorsolateral sulcus
..... *Penaeus (Farfantepenaeus)* Burukovsky, 1972
- Gastrofrontal carina turning anterodorsally at posterior end; sixth abdominal tergite without dorsolateral sulcus 3
- 3 Telson lacking lateral spines *Penaeus (Plagosopenaeus)* subgen. nov.
- Telson armed with 3 pairs of movable lateral spines 4
- 4 Postrostral carina without median sulcus; usually 2 ventral rostral teeth
..... *Penaeus (Altiopeneaus)* subgen. nov.
- Postrostral carina bearing median sulcus; usually 1 ventral rostral tooth 5
- 5 Median sulcus at postrostral carina distinctly shorter than half carapace length; first pereiopod armed with strong ischial spine
..... *Penaeus (Ischiopeneaus)* subgen. nov.
- Median sulcus at postrostral carina more or less as long as half carapace length; first pereiopod with ischial spine minute or absent 6
- 6 Cervical carina with dorsal end almost reaching dorsal carapace
..... *Penaeus (Melicertus)* Rafinesque, 1814
- Cervical carina with dorsal end a distance from dorsal carapace 7
- 7 Thelycum pouch-like; posterior part of adrostral sulcus somewhat narrower than postrostral carina; body banded
..... *Penaeus (Marsupenaeus)* Tirmizi, 1971
- Thelycum closed but not pouch-like; adrostral sulcus as wide as postrostral carina; body not banded *Penaeus (Oleopenaeus)* subgen. nov.
- 8 Hepatic carina absent or ill-defined
..... *Penaeus (Fenneropenaeus)* Pérez Farfante, 1969
- Hepatic carina distinct 9

9	Fifth pereiopod without exopod; hepatic carina nearly horizontal
	<i>Penaeus (Penaeus) Fabricius, 1798</i>	
-	Fifth pereiopod bearing exopod; hepatic carina usually sloping anteroven-trally	10
10	Thelycum open; dorsolateral sulcus, though sometimes rather weak, present on sixth abdominal somite	<i>Penaeus (Litopenaeus) Pérez Farfante, 1969</i>
-	Thelycum closed; dorsolateral sulcus completely absent on sixth abdominal somite	<i>Penaeus (Eopenaeus) subgen. nov.</i>

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